The Development of Vegetation in the English Lakes, considered in relation to the General Evolution of Glacial Lakes and Rock Basins.*

By W. H. PEARSALL.

(Botany Department, University of Leeds.)

(Communicated by A. G. Tansley, F.R.S. Received April 28, 1921.)

Introduction.

During the past seven years, 1913–20, a large number of observations have been made in the English Lakes in an attempt to obtain some knowledge of the life conditions of aquatic plants. While the immediate object was to obtain light on the factors governing the distribution of these plants, it was also hoped that the results might bear upon more general problems of aquatic biology. The considerable data thus obtained, though far from complete, seem to be of interest from both these points of view. They are also capable of a more general interpretation, which is here attempted, and which, for the sake of clearness, may be indicated at this stage.

It is assumed that lakes and lake basins become modified as they increase in age. Evidence is then presented for considering the English Lakes as a series illustrating this process of lake development, and an attempt is made to describe the phases in this process, and to relate the marked differences in lake vegetation and fauna to the stages in the topographical evolution of a lake.

The data given below refer to the normal summer conditions of these lakes, and the methods employed in obtaining them have been described in a previous paper.[†] The arduous work of surveying the lake shores has only been possible through the unsparing assistance of my father, W. Harrison Pearsall, to whom I am very greatly indebted. The water analyses given were undertaken by Messrs. A. W. Richardson and R. Jaffé, to whom my thanks are due.

General Features of the Lakes and Lake Area.

The English Lakes lie among the high hills of Cumberland, Westmoreland, and North Lancashire. These hills consist essentially of a central uplift,

---

[*] The cost of this investigation has been defrayed in part by grants from the Royal Society.

[†] Pearsall, "The Aquatic Vegetation of the English Lakes," 'Journ. Ecol.,' vol. 8, 1920.

from which run out ridges, radiating like the spokes of a wheel, and gradually decreasing in height as they pass further away from the centre. Practically all the main valleys between these ridges contain one or more lakes, varying greatly in size, but otherwise somewhat similar in appearance and characteristics. It is with eleven of the larger lakes that the present paper deals; Thirlmere, now practically a reservoir with variable water level, and those lakes smaller than Buttermere, having been omitted for the sake of uniformity. The remaining lakes vary in length from 10·5 miles (16·8 kilom.) (Windermere) to 1·26 miles (2 kilom.) (Buttermere), and have mean breadths of from 0·5 to 0·25 miles (0·8 to 0·4 kilom.). They lie at uniformly low altitudes, Hawes Water, 694 feet (211 m.), being the highest. Our knowledge of their chief sub-aqueous features is due to the work of Mill and Heawood,* from whom the table of their dimensions (Appendix I) is chiefly compiled.

Origin of the Lakes.—As is well known, the whole of the Lake District was very heavily glaciated during the Ice Age, with the result that soil, surface deposits, and all but the boldest features of pre-glacial scenery, were removed by ice, leaving a bare and sterile rock mass, here and there overlaid by moraines and boulder clay. The effects of ice were particularly striking in the valleys. These were deepened and scoured out, the greatest erosion taking place towards the heads of the depressions, where the valleys (and the ice) were deepest. Thus, on the retreat of the ice, a number of *rock basins* were left, occupying the lines of the pre-glacial valleys, and tending to have straight steep sides, all minor points having been torn away by the ice and removed, along with any pre-glacial alluvial deposits (see Marr).†

The present lakes lie in these rock basins, and it may be noticed that the theory of their origin presupposes that their primitive condition was essentially *rocky*, a supposition borne out by the nature of the shores and islands at the present day. Glacial deposits also frequently exist, often rounded morainic boulders, and sometimes an impervious boulder clay. Neither the presence of these, nor the fact that they may hold up the lake to a higher level (as at Windermere and Bassenthwaite), invalidates the conception that these lakes are essentially rock basins, and are, in origin, of great similarity.

Modifying Agencies.—*Wave action* produces numerous well marked effects. Along the shores one can typically distinguish three chief zones caused by wave action: (1) the *gravel* wave-cut terrace just below the water level (2) a comparatively silt-free area of stone or boulder clay, often sprinkled with *sand;* (3) a silted (and more or less muddy) zone in deeper water. Generally, the stones or gravel of the terrace extend to about 2 m. in depth, while the finer sands and silts lie below 4 or 5 m. The finest sediments tend to get carried along the shore by the littoral current, and they are deposited in bays or holes, where this current slows down as it passes into deeper water. It follows, therefore, that bays and holes tend to get silted up—points and exposed shores to be kept silt-free. Since the lakes are of different lengths and lie at different angles to the prevalent winds (here S.W.), the strength of wave action varies very greatly, and its results are shown in very different degrees. For instance, wave effects are most severe in Wastwater, Coniston, Windermere and Ullswater, all long lakes lying roughly S.W. to N.E.

---

* 'Geogr. Journ.' (London), vol. 6, 1895.

† 'The Geology of the Lake District,' Cambridge, 1916.

A second type of modification is produced in any lake by the presence of *fluvial* sediments. The lateral affluents of lakes lying in such steep-sided valleys as these are normally rapid, and carry down into the lakes quantities of coarse detritus, chiefly gravel. The mouth of every small stream thus, in time, projects into the lake on a gravel delta, and as a lake increases in age, its shores tend to become more and more irregular owing to the development of these deltas. It then follows that parts of the shores become sheltered and more silted than they otherwise would be.

This modification of the lake shores is only one sign of the effects of regional erosion and this group of factors produces other changes in the characters of the lakes. As the surrounding country weathers from crag and scree into gentle slopes and soil, the gradients of the streams tend also to decrease and their carrying power is diminished, particularly where they enter the lake. Hence, they ultimately carry into the lakes, not gravels but *silts,* and since the surrounding country is developing soil as it becomes more eroded, *finer silts tend to become available in increasing quantities,* replacing the sands and gravels of the earlier stages of lake development.

Geology of the District.—As the map shows, three main types of strata exist—to the north, the Skiddaw slates; in the centre, the volcanic ashes and lavas of the Borrowdale series; and in the south, a group of Silurian slates, grits and flags. In their appearance and general characters, these three types of rocks are very similar, but though all are hard, the central volcanic rocks are harder than the sedimentary rocks of the Silurian and Skiddaw beds, and, moreover, possess larger and more regular joints. Hence they weather more slowly, and also give rise to block screes, rather than to finer products. The effect of this upon the topography of the district is very noticeable. Having weathered least, the central hills tend to be higher, more rocky and steeper, while around them lie the lower and more eroded hills of the softer strata, usually round-topped and covered more or less with soil. So, too, the lakes on or near the central harder mass tend to be more rocky, while on the softer strata they are more silted. Some of the bolder slopes and the more rocky lakes may, however, lie on the Skiddaw slates (*e.g.*, Buttermere, Crummock and Derwentwater) and hence, it seems clear that it is *the degree of erosion of the surrounding country which largely governs the present physical condition of the lakes.*

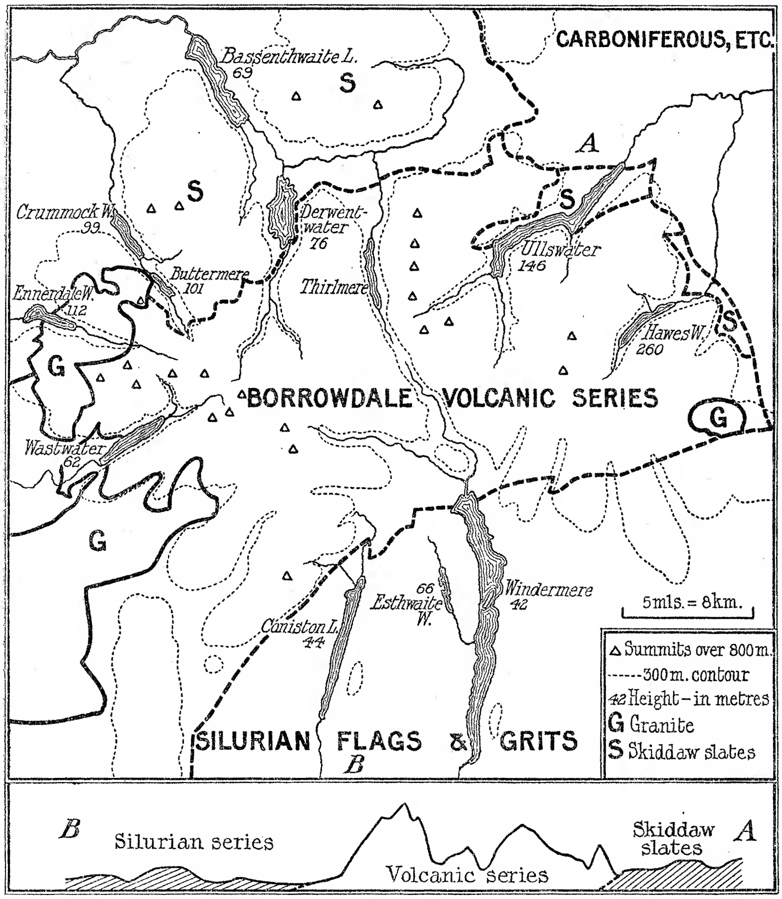

Fig. 1.—Map of the English Lake District, with section showing the relation of scenery and gradients to the underlying rocks.

An endeavour has been made to express numerically the differences arising from these conditions of erosion, the results being included in Table I. As an expression of the types of slopes and soil-covering of the surrounding country, the percentage of cultivated land and alluvial pasture is given for the drainage system of each lake. The steeper slopes are either screes or rough pasture, the flatter hill tops are usually moorland. Only alluvia and the gentler soil-covered slopes can be cultivated, and hence the above ratio, though rough, is a fairly accurate expression of the character of the drainage system. From the figures given, it will be seen that the lake drainage systems fall into two classes, characterised by low and high proportions of cultivable land respectively.

Table I.—Effects of Erosion.

Lake.	Percentage of drainage system cultivable.	Lake shore to 30 feet depth. Per cent. rocky.	Relative transparency of lake water.
			m.
Wastwater	5·2	73	9
Ennerdale	5·4	66	8·3
Buttermere	6·0	50	8·0
Crummock	8·0	47	8·0
Hawes Water	7·7	25	5·8
Derwentwater	10·0	33	5·5
Bassenthwaite	29·4	29	2·2
Coniston	21·8	27	5·4
Windermere	29·4	28	5·5
Ullswater	16·6	28	5·4
Esthwaite	45·4	12	3·1

The second column in this Table shows the approximate proportion of the shore-line of each lake, which is rocky. From the soundings along the shores the average depth to which stones or rock extend has been determined, the deeper part of the shores being silted and soft. Taking 30 feet (9·2 m.) as a maximum, the percentage of the shore-line which is rocky can thus be obtained very approximately for each lake.

As the soundings on which these are based were made chiefly in bays, the figures given are possibly too small. They are, however, truly comparable. While the small size of Esthwaite may be the cause of the silted nature of its shores, as compared with Coniston, Windermere, and Ullswater, it cannot be assumed that the high degree of silting in the latter lakes is due to the slight effects of wave action, for Derwentwater, both smaller and with more irregular shores, has more rocky shore-lines. Similarly, Wastwater, in which the degree of wave action is almost the same as in Windermere, has shores which are much less silted. By comparison with the first column in the Table it will be seen that the *rocky* lakes (Wastwater to Crummock) lie among steep slopes and uncultivated land, the *silted* lakes (Derwentwater to Esthwaite) lie among the gentler soil-covered slopes. It seems a fair assumption, then, that the character of the shore-line, whether silted or rocky, depends largely upon the character of the surrounding country; but it should also be remembered that the softer rocks along the shores of the more silted lakes are more easily eroded by waves.

Another criterion of the silting conditions in any lake may be employed. Since suspended matter makes water more opaque, the relative transparency of the lake waters may be used as an indication of the quantity of suspended matter they contain. The basis of the comparison is taken as the greatest depth at which a white disc (7 cm. in diameter) can be seen. The results are contained in the third column of Table I, and they show that the clearest waters occur in those lakes with rocky shores. The test must be used with caution, for some of the lake waters are coloured with dissolved peaty matter, *e.g.*, Bassenthwaite and Esthwaite. But it is permissible to conclude from these results that there are greater quantities of suspended matter in the waters of those lakes with silted shores. Moreover, since only the finest matter can remain long in suspension, the greater opacity of the waters of these lakes indicates that their affluents bring in material *in a finer state of subdivision than that carried into rocky lakes.* It has already been shown that this is *a priori* probable. Further evidence in support of this assumption is obtained by comparing the mechanical analyses of muds taken from Wastwater, the most rocky lake, with those taken from Esthwaite, the most silted lake. The following results are then obtained:—

Table II.—Mud Analyses.

Material.	Wastwater (rocky). Per cent.			Esthwaite (silted). Per cent.			
Sand	75·1	82·8	74·9	62·0	54·2	34·2	28·2
Silt	14·8	15·0	16·1	17·6	14·6	29·3	25·3
Fine silt and clay	10·1	2·2	9·0	20·4	31·2	36·5	46·5
	1	2	3	4	5	6	7

The muds for these analyses were all obtained from depths of 8 to 12 feet (2·4 to 3·6 m.), so that they are fairly representative. The varying forces of wave action make an exact comparison very difficult, but the differences are sufficiently striking to make it probable that the sediments of *rocky* lakes tend to be *coarse,* while those of *silted* lakes tend to be *finer.* Field notes are quite in agreement with this conclusion.

Thus on their physical characters alone the lakes can be divided into two extreme types, *rocky* and *silted.* Wastwater, Ennerdale, Buttermere, and Crummock represent the *rocky* type, while Coniston, Windermere, Ullswater, and especially Esthwaite, belong to the *silted* type. Derwentwater, Bassenthwaite, and Hawes Water remain as intermediate examples between the two extremes. Other attributes of these lakes will now be considered.

Chemical Characters of the Lake Waters.

Chemically the waters of these lakes possess much in common (see Appendix II). They are notably poor in dissolved minerals, and particularly in calcium and carbonates. Other ions, therefore, constitute an unusually large proportion of the dissolved matter, particularly those of the alkalies (Na and K), an unusual feature in pure natural waters. The sulphate-content is high in the case of Crummock, Buttermere, Bassenthwaite, and Esthwaite, the only lakes where drainage systems lie entirely on the Skiddaw and Silurian rocks. In other respects, the influence of various strata is not very apparent and the only satisfactory classification is obtained by arranging the lakes in the two groups, *rocky* and *silted,* as already distinguished. It then appears that:—

(1) The waters of the rocky lakes have a high ratio of $\frac{Na_2O+K_2O}{CaO+MgO}$.

(2) The waters of silted lakes are characterised by larger quantities of nitrates, carbonates and silica.

(3) The latter waters tend also to possess larger proportions of lime and organic matter.

All the variations thus observed between the two types of water can apparently be related to the physical differences in the lake-basins and their drainage systems. The ratio $\frac{Na_2O+K_2O}{CaO+MgO}$ is chosen to represent the difference in the character of the bases. The tendency for the ratio to be low in silted lakes is probably in part due to the adsorption of K by sediments. The following facts bear out this assumption. While in Ennerdale and Wastwater potassium constitutes 50 to 60 per cent. of the whole K-Na residue, in Esthwaite and Ullswater it rarely exceeds 20 per cent. It is, moreover, well known that the drainage water from normal soils rarely contains much K, owing to the adsorption of this ion by the electro-negative soil colloids, and the same effect is produced when soil particles (*i.e.*, silts) are suspended in water containing traces of potassium. It has been shown already that the silted lakes are surrounded by greater areas of fertile soil, and possessed of greater quantities of suspended matter in their waters, and it may therefore be assumed that greater quantities of potassium are adsorbed by silts from the waters of these silted lakes, in comparison with those of rocky lakes. In addition, silted lakes possess *finer* sediments than rocky ones, and it is found that the finer silts contain larger proportions of potash than the coarser

(Table III). Finally, silts deposited from the lake waters are uniformly richer in potash than are the unaltered sands and glacial " clays " of the lake floors, *e.g.*, Nos. 2, 14, 16, Table III.

Table III.—Proportions of Potash.

No.	Sand.	Silt.	Fine silt.	K_2O.	No.	Sand.	Silt.	Fine silt.	K_2O.
5	34·2	29·3	36·5	0·0535	10	73·4	19·2	7·4	0·0290
7	69·2	14·6	21·2	0·0462	13	71·7	14·1	14·2	0·0260
23	44·9	29·1	26·0	0·0410	9	76·6	14·0	9·4	0·0232
20	51·5	28·4	20·1	0·0370	15	82·8	15·0	2·2	0·0232
6	72·0	7·6	20·4	0·0342	11	76·8	18·0	5·2	0·0228*b*
8	64·2	23·6	12·2	0·0338	2	63·1	16·1	20·8	0·0220
19	70·9	14·1	15·1	0·0336	14	78·0	10·9	11·1	0·0210 *a*
12	65·3	24·5	10·2	0·0301	16	75·1	14·8	10·1	0·0202

Figures as percentages. *a*, Boulder clay with slight silt; *b*, slight silt over stones.

Hence it may be inferred that fine silts adsorb potassium from the lake waters, resulting in a decrease in the ratio $\frac{Na_2O + K_2O}{CaO + MgO}$ as the lake becomes more silted. It may be noted that the adsorption of K would be accompanied by a liberation of Ca and Mg into solution.

The increase of carbonates, nitrates and silica in the silted lake-waters is apparently due also to the effects of silting. The development of soil in the drainage system and of silts in the lakes may be assumed to be followed, in each case, by the development of vegetation. Organic matter deposited is then decayed under the aerobic conditions of the soil, forming CO_2 and nitrates. If the soils are rich in bases, complete decomposition results instead of the partial disorganisation which results in the formation of peat. Similarly sub-aqueous silts rich in potash are characterised by organic matter decaying rapidly and completely, while coarser potash-poor silts accumulate organic matter which is relatively undecayed. (Nitrates are formed in potash-rich silts.) It is apparently correct, therefore, to assume that the adsorption of potassium by silts results in the acceleration and completion of the processes of decay, and the formation of increased quantities of CO_2 and nitrates, the end products of these processes. Thus it follows that the silted lake waters contain greater quantities of carbonates, nitrates and usually of organic matter, and we can probably attribute their higher proportions of silica, calcium and magnesium, in part, to the solvent action of CO_2. (There is, of course, a resultant decrease in the $\frac{Na_2O + K_2O}{CaO + MgO}$ ratio.) Thus clearly the main differences between the lake waters are closely related to the degrees of silting of the lakes.

General Conclusion.—A conclusion of even more significance is now permissible. The fact that these lakes lie in glacial rock-basins entitles us to assume that at the close of the glacial period their condition was more uniformly rocky than it is to-day. Lakes lying on the hardest rocks have changed least, they are still rocky and *relatively primitive.* Lakes lying on softer strata are now more silted and therefore *more highly evolved.* It is thus possible to consider the group of lakes as a series illustrating the stages in *the post-glacial development of a typical rock basin lake,* a conception of great value, since it enables us to study the stages in development of a post-glacial fauna and flora.

On this assumption, Wastwater and Ennerdale are most primitive, and probably are not greatly altered from their immediate post-glacial condition. Windermere, Ullswater, and particularly Esthwaite, are most highly evolved, the remaining lakes exhibiting various intermediate stages, of which Derwentwater is perhaps the most valuable. In adopting this view, it must be admitted that the topography of the extremely evolved lake basins—notably of Esthwaite—was probably never so primitive as that of Wastwater. This, however, affects the *degree* of evolution only; it does not affect its *direction,* which, in lakes lying among similar rocks, and relatively uniform glacial deposits, must have proceeded along the same main lines.

We can now apply this theory of lake development to the distribution of the aquatic vegetation.

Vegetation.

The vegetation of a lake area falls conveniently into two main groups:—(1) attached plants, or *benthos;* (2) free-floating plants, or *plankton.*

Benthos.—The distribution of the characteristic deep-water plants in these lakes is shown in Table IV, the numbers given representing percentages of the total deep-water flora. For convenience, the species are divided into three groups:—

(A) Primitive plants: *Isoëtes* and *Characeæ.*
(B) Silt-requiring plants: *Juncus, Callitriche,* and *Potamogeton.*
(C) Plants of organic soils: *Myriophyllum,* etc.

Elodea can be placed in both (B) and (C).

As most of the soundings on which these figures are based were made in bays, the proportions given for plants in group B are probably too high, but the results are comparable, since the same error exists in each tabulation.

An analysis of the habitat conditions under which these plants live shows that their distribution depends upon the characters of the substratum rather

Table IV.—Plants Growing below Depths of 2 m.

The numbers represent percentage occurrences, *i.e.*, the ratios of total records of each species, to total records of all species (taken as 100).

	Wast-water.	Enner-dale.	Butter-mere.	Crum-mock.	Hawes Water.	Derwent-water.	Bassen-thwaite.	Coniston.	Winder-mere.	Ulls-water.	Esthwaite.
A. *Isoëtes lacustris* L.	49	35	40	48	5	31	42	34	9	34	2
Nitella opaca Ag. }	36	46	40	26	65	42	3	9	40	15	26
N. flexilis Ag. }											
Chara fragilis Desv.	—	2	—	—	6	1	—	—	3	—	2
Total	85	83	80	74	76	74	45	43	52	49	30
B. *Juncus bulbosus*, L., *f. fluitans*, Lam.	6	5	7	8	1	7	2	2	—	—	—
Callitriche intermedia, Hoffm.	2	1·5	3	5	4	1	21	7	0·5	—	1·5‡‡
Potamogeton pusillus, L.	0·5‡	0·5	1‡	2	2	1	3	15	3	10	6·5
P. perfoliatus, Wulf.	—	—	—	—	0·5	4	—	13	11	17	11
P. prælongus, Wulf.	—	—	—	—	—	1	—	2¶	14	8	1
Total *Potamogeton* spp.	0·5	0·5	1	2	5§	6	3	30	29††	35	25·5§§
Elodea canadensis, Mich.	—	—	—	—	—	—	—	—	9	—	10
Naias flexilis, R. and S.	—	—	—	—	—	—	—	—	—	—	21‖‖
C. *Myriophyllum* spp.*	6·5	10	9	8	13	2	11	6	4	14	2¶¶
Utricularia spp.	—	—	—	—	—	7‖	—	1**	—	—	—
Fontinalis antepyretica, L.	—	—	0·5	1	1	2	2	6	—	—	6
Other mosses	—	—	—	2	—	1	2	2	—	0·5	—
Ranunculus spp.†	—	—	—	—	—	—	12	2	1	2·5	—
Sparganium minimum, Fr.	—	—	—	—	—	—	2	1	1·5	—	4

* Chiefly *M. spicatum*, L.
† Probably *Ran. truncatus*, Koch.
‡ Including *P. polygonifolius*, Pourr., var. *pseudofluitans*, Syme.
§ Including *P. crispus*, L.
‖ Probably *U. major*, Sch.
¶ Also *P. alpinus*, Balb., and *P. zizii*, Koch.
** *U. intermedia*, Hayne.
†† *P. alpinus*, Balb., and *P. obtusifolius*, M. and K.
‡‡ *C. autumnalis*, L.
§§ Also *P. obtusifolius*, M. and K.
‖‖ *Naias*, 17 per cent.; *Hydrilla verticillata*, Casp., 4 per cent.
¶¶ *M. alterniflorum*, D.C.

than upon variations in the composition of lake waters or in the physical conditions of the habitat.*

Table V summarises the soil types upon which the more important species are found:—

Table V.—Species and Soils.

Plant community.	No. of samples.	Fine silt and clay percentage.		"Available" potash percentage.		Rate of silting.
		Range.	Average.	Range.	Average.	
Isoëtes lacustris	4	5 ·2–20 ·8*	11 ·8	0 ·020–0 ·023	0 ·021	Very slow.
Juncus fluitans...	5	2 ·2–14 ·0	7 ·5	0 ·023–0 ·029	0 ·025	Moderate.
Callitriche intermedia	3	7 ·4–16 ·5	12 ·6	—	—	"
Potamogeton perfoliatus	3	10 ·2–20–4	15 ·2	0 ·030–0 ·034	0 ·033	"
P. pusillus and *P. prælongus*	6	12 ·2–36 ·8	22 ·5	0 ·034–0 ·053 (4)	0 ·042	Rapid.
Naias flexilis ...	—	36 ·5 and 46 ·5	41 ·6	0 ·054	—	"

* A little altered boulder clay.

It will be seen that *Isoëtes* and *Juncus fluitans* occur on the coarser soils, poor in available potash, while *Potamogeton* and *Naias* are found on the finer and richer silts. The decrease in abundance of *Isoëtes* and *Juncus* in evolved lakes can therefore be attributed to the development of *Potamogeton* spp., consequent upon the increased abundance of finer and richer sediments.

It has further been shown that the development of silting on a lake shore leads to the replacement of *Isoëtes* by *Nitella*, which requires an easily penetrable substratum. Where sediments are abundant and the mud deep, higher plants (of group B) replace *Nitella*.* The gradual decrease of the primitive plants from 85 to 30 per cent. in the lake series is due, therefore, to the silting up of the shores in the evolved lakes, and to the greater rate of sedimentation.

It may be noticed, finally, that, including *Elodea*, the plants of the more organic soils become more abundant and more varied in evolved lakes, which have presumably been colonised by plants for the greatest period of time.

The peculiarities of individual lakes may now be considered, to explain the variations in Table IV. The frequencies given for any species are based on the total records for the lake, reduced to the same relative proportions of the lake flora as in Table IV.

The Development of Vegetation (fig. 2).—In Wastwater and Ennerdale, both *Isoëtes* and *Nitella* are most often found at a depth of about 6 m., and have similar ranges of depth. The plants are normally rather scattered, and obviously colonising bare areas. Very large parts of the lake shores are devoid of vegetation. The depth distribution of *Isoëtes* and *Nitella* is remarkable when it is considered that, while the light limit for vegetation in these two lakes must be at least 10 m., probably more, yet little vegetation occurs below 7 m., or, normally, above 3 m. The development of vegetation between these two depths is undoubtedly due to the fact that wave-formed sediments are deposited more commonly at 4 to 7 m., while above this zone rocks are found, and below it rocks or glacial till. In well sheltered bays or near streams, the zone of silts may be much more extensive, and there the vegetation is correspondingly more widely spread. On the abundant sands near stream mouths, *Juncus fluitans* replaces *Isoëtes* and *Nitella,* and *Littorella* may be found locally on wave-beaten gravel. Normally, however, there is little zonation of different types of vegetation.

---

* Pearsall, *loc. cit.*

Great differences are apparent when the Derwentwater figures are examined. *Nitella* is still most abundant at the same depth, but its downward extension is curtailed by light conditions. It is becoming more abundant in shallow water and, as in Windermere and Ullswater, its upper limit coincides roughly with that of the mean silted area. Rocks are rarely found below 5 m. *Isoëtes* is now most abundant in much shallower water—2·3 to 3·6 m.—and has obviously been replaced at greater depths by the combined effects of silting and *Nitella* competition, while its further extension into shallow water is stopped by the development of the *Littorella* zone on marginal gravel and sand. It is, in fact, confined to the least eroded and least silted parts of the shores, *i.e.,* the most primitive. This is the usual type of distribution of *Isoëtes* and *Nitella* in these lakes, and it is *due to the physical conditions of the lake shores.* Where, as in Ennerdale, the moulding and silting of the shores has progressed but little, and the waters are very clear, one may find *Isoëtes* below *Nitella* as well as above, the *Nitella* coinciding with the zone of maximum silting. A similar less frequent example in Ennerdale gives:—

(1) *Littorella,* abundant on gravel and sand to 4 m.
(2) *Nitella,* abundant on deep fine sand and silt, 3 to 5 m.
(3) *Isoëtes* abundant on little altered glacial clay, 5 to 8 m.

Returning now to Derwentwater, here again the higher plants, *Juncus fluitans* and *P. perfoliatus,* are chiefly confined to shallow water on abundant sediments near stream mouths, the appearance of *P. perfoliatus* being attributed to the finer nature of the silts. Small quantities of *Potamogeton* are also appearing in deep water, replacing *Nitella.*

In Windermere all these processes have progressed much further, as silts are much more abundant. Owing to the great development of *Littorella* and *Nitella*, *Isoëtes* is relatively scarce, while *Juncus fluitans*, in its deep-water form, is quite absent. *P. perfoliatus* and *Elodea* are becoming abundant in the region formerly occupied by *Isoëtes* (*e.g.*, Derwentwater), while *P. prœlongus* and *P. pusillus* are becoming abundant in the *Nitella* region. All of these changes are attributable to the increase in abundance and fineness of the silts.

In Ullswater the abundance of *Potamogeton* causes a very marked reduction in the quantity of *Nitella*. Here, again, *P. perfoliatus* is developing where the *Isoëtes* zone is becoming silted (*i.e.*, in bays). If the development of these lakes followed an exact sequence, *Isoëtes* should be nearly absent from Ullswater, as it is in Esthwaite; but an impenetrable glacial till is common in Ullswater, which, unless removed by wave action, prevents the extension of *Littorella*, *Potamogeton*, or *Nitella*. The persistence of *Isoëtes* on these primitive substrata is one of the features of Ullswater (and Coniston) and partly accounts for the abundance of that species. The point will be discussed in more detail below.

Esthwaite, for which no diagram is given, shows a further advance on the Windermere stage, *Isoëtes* being nearly absent, and *Nitella* encroaching on the *Littorella* zone to depths of 1 to 1·5 m. In Esthwaite other higher plants (particularly *Naias flexilis*) are numerous, to some extent replacing *Potamogeton*.

In primitive lakes higher plants only occur on abundant coarse fluvial sediments in rather shallow water, and they are confined to a few localities in each lake. Their development as deep-water plants along the shore-line only occurs when silts become abundant, and there is a marked tendency for the plants to progress into shallower water, already noticed for *Isoëtes* and *Nitella*, and clearly due to the increased silting of the shores. The case of *P. perfoliatus* is a good instance of this point (see fig. 2). It is worthy of notice that the first *Potamogeton* to appear in quantity is *P. perfoliatus*, which normally occurs on coarser and poorer silts than *P. prœlongus* or *P. pusillus*.

The examples considered above make it apparent that the zonation of aquatic plants along a shore is an attribute of evolved lakes, and is, moreover, primarily dependent upon the condition of the substratum as determined by the silting factor. Were one alone of these lakes to be considered, it might well be assumed that zonation was due to light conditions, but such a conclusion is difficult to reconcile with the series described above. This is equally well shown when a series of lengths of shore in a single evolved lake is examined. Generally speaking, the variations described above would be found, provided conditions of exposure varied sufficiently. Thus, an exposed shore would show the Wastwater or Derwentwater stages, a sheltered one the Windermere or Ullswater condition, though the range of light intensities at different depths would be similar in each case.

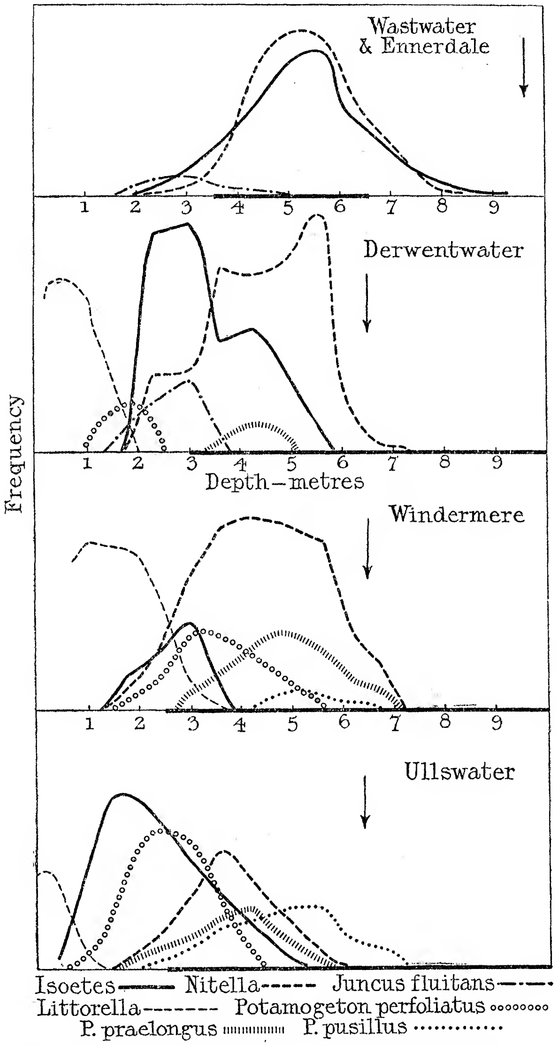

Fig. 2.—Depth distribution of characteristic species in the lakes named. The arrows show the light limit for vegetation. The thickened base line indicates the parts of the lake shores normally silted. The frequencies for any species are based on the total records for the lake, reduced to the relative proportions of Table IV.

Apparent Exceptions: Hawes Water.—This lake is apparently abnormal (i) in its high proportion of *Nitella*, *Isoëtes* being scarce, (ii) in the high percentage of its shore-line that is silted. It may be remarked that the second abnormality explains the first, since silting tends to replace *Isoëtes* by *Nitella*.

Both features can be accounted for by the fact that Hawes Water *has been heavily silted in the past,* shown not only by the condition of the lake floor but also by the size of the gravel alluvia at the mouths of the two main affluents. Moreover, in marked contrast to the gravel deltas in other lakes in this district, those at Hawes Water show no signs of recently deposited gravel. Mill (*loc. cit.*) also points out, quite justifiably, that the Measand Delta could never have been laid down by the present stream, and he attributes its formation to the "washing out" of a glacial lake. The third point of interest is that the sediments of Hawes Water are fine *sands,* not silts* such as would be carried into a lake by torrential streams. Very vigorous erosion in the past seems, therefore, to have washed huge quantities of sand and gravel into Hawes Water. The sand helped in the silting-up of the shores, it allowed the replacement of *Isoëtes* by *Nitella,* but it is too coarse to allow the extensive development of *Potamogeton,* spp. Thus Hawes Water, though abnormal, is not at variance with the views expressed previously.

Bassenthwaite owes its peculiarities to the brown and peaty nature of its waters, a coloration due to the extensive peaty alluvia at the lake head. The water is so discoloured that the lower light limit of vegetation is only 2·5 m., and the fine deeper water sediments cannot be colonised by plants. Owing to wave action, silting is naturally less rapid in shallow water, and moreover the sediments are coarser and become rapidly organic, owing to the slower deposition of silts, and their comparative poverty in potash. Thus, the vegetation of such a lake will be that characteristic (*a*) of wave-washed shores (little silted), (*b*) of the coarser sediments, (*c*) of the more organic sub-strata. The plants occurring in such habitats are (*a*) *Isoëtes,* (*b*) *Callitriche intermedia,* (*c*) *Myriophyllum* and *Ranunculus,* all of which are abundant in Bassenthwaite. The absence of the finer and softer sediments within the photic zone accounts for the scarcity of *Potamogeton* and *Nitella,* spp.

Coniston and *Ullswater* resemble Bassenthwaite in possessing a relatively high proportion of *Isoëtes,* yet their light conditions are normal and both include abundant *Potamogeton.* An examination of Table I shows that both lakes have a smaller percentage of cultivable land in their drainage systems than is compatible with the degree of silting, *i.e.*, their drainage systems are more primitive than the lake basins. It has already been remarked that their abundant silts are largely due to washings from lead or copper mines, and it is known, of relatively recent times. The coarser silts from such washings smother the lake floor round the mouth of the incoming streams, the finer are deposited all over the lake floor, *except in the regions subject to wave-wash, i.e.*, on most of the lake shores between the water margin and depths of 3 or 4 m. These wave-washed areas can only accumulate silt during calm weather, and hence change their character very slowly. Thus the discharge of ore washings into these lakes would cause an abundance of fine silts in deep water, and this would result in the replacing of *Nitella* by *Potamogeton* spp. On the other hand, the shallower water soils would remain little altered, and would retain their primitive vegetation of *Isoëtes.* Another factor tends to accentuate the retention of this primitive shore line in Ullswater and Coniston. The shores are relatively straight, as compared with Windermere and Derwentwater, and hence, offering no obstacles to the sweep of waves and littoral currents, are kept comparatively silt-free at depths of less than 3 to 4 m.

---

* *Cf.* also Mill, *loc. cit.*

Shallow-Water Vegetation.—In the case of the shallow-water plants, much greater difficulty is experienced in making a comparative table of distribution. These plants are directly affected by wave action, and they are therefore very closely dependent upon the degree of exposure of the lake shores. In lakes like these, varying greatly in size, orientation and shelter, a direct numerical comparison is therefore impossible, and only the presence or absence of typical plant communities can be given :—

Table VI.—Distribution of Shallow-water Plants.

	Wastwater.	Ennerdale.	Buttermere.	Crummock.	Derwentwater.	Hawes Water.	Bassenthwaite.	Coniston.	Windermere.	Ullswater.	Esthwaite.
Littorella lacustris, L.	+	+	+	+	+	+	+	+	+	+	+
Potamogeton (submerged), spp.*					+				+	+	+
Myriophyllum spicatum, L.					+	+	+	+	+	+	+†
Ran. peltatus, Schr.							+	+	+	+	+
Potamogeton natans, L.‡				+	+	+	+	+	+	+	
Water-lilies§					+		+	+	+		+
Phragmites communis, Trin.				+	+	+	+	+	+	+	+
Scirpus lacustris, L.											
Equisetum limosum, L.		+	+	+	+	+	+	+	+	+	+
Carex inflata, Huds.											

* *Potamogeton gramineus*, L. (agg.), × *P. nitens*, Weber., *P. perfoliatus*, L., *P. alpinus*, Balb.
† *M. alterniflorum*, D.C.
‡ Including occasional *Castalia minor*, D.C.
§ *Nymphæa lutea*, L., and *Castalia alba*, Wood.

Even this rough method of comparison indicates that shallow-water plants are more typical of evolved than of primitive lakes, in spite of the considerable variations observed. Derwentwater, with a broken shore-line and numerous islands, is comparatively rich in this type of vegetation, and of the emergent species, *P. natans*, with the *Equisetum-Carex* type of reedswamp, predominate, though *Scirpus* and *Phragmites* are also abundant. The same plants are characteristic of Hawes Water and Bassenthwaite, though much less abundant. In Coniston and Windermere, *Scirpus* and *Phragmites* are more typical, along with some *P. natans*. In Esthwaite, water-lilies and *Phragmites* fringe most of the western shore. On the whole, as silting conditions improve, water-lilies and *Phragmites* tend to become more abundant in the lake series, a fact in agreement with their distribution on relatively inorganic soils, which are relatively richer in K_2O.* *P. natans*, *Equisetum* and *Carex inflata*, on the other hand, are found on highly organic soils, relatively poor in K_2O. Obviously, the increased development of finer and richer silts in evolved lakes tends to prevent the formation of these highly organic soils, except in land-locked and stagnant bays—which are uncommon in this lake area. It is therefore primarily to the silting factor that the development of both deep and shallow water vegetation is due.

General Conclusion.—This detailed discussion shows clearly that the fundamental factor in the development of the attached vegetation is the increase in abundance and richness of the sediments. Not only does this control the types of plant communities found, but it also limits the quantity of vegetation produced. Vegetation is sparse in the primitive lakes; it becomes increasingly abundant in the evolved lakes. As was suggested at the conclusion of the last section (p. 267), the lake series viewed in this way enables us to reconstruct the stages in the post-glacial development of these lakes. If this be done for the vegetation, we obtain the following means for the four main types of lake, and these represent four stages in the development of a post-glacial flora :—

Vegetation Types.

	Type of lake.			
	I. Primitive (4).	II. Intermediate (3).	III. Evolved (3).	IV. Esthwaite.
Primitive plants— *Isoëtes* and *Characeæ*	80·5	65	47·6	30
Juncus and *Callitriche* (requiring coarse silts)	9·4	11·9	3·1	—
Potamogeton spp. (requiring finer silts)	1·0	4·6	31·3	25·5
Naias, *Hydrilla* and *Elodea*	—	—	3·0	21·0

---

* Pearsall, *loc. cit.*

Phytoplankton.—While no data are available for an accurate numerical comparison of the phytoplankton of these lakes, the investigations of W. and G. S. West* have already drawn attention to the fact that differences in its composition exist. The Wests' investigations included all the larger lakes except Coniston and Esthwaite. In addition, they described the periodicity of three lakes—Wastwater, Ennerdale and Windermere.† The following Table gives the maximum abundance of a few conspicuous plankton

Table VII.—Maximum Recorded Abundance of Principal Plankton Algæ.*

Wastwater	Desmids dt. (*Staurastrum jaculiferum*, West.); *Peridinium Willei*, Huit. Kaas and *Sphærocystis Schroeteri*, Chodat. ab.; *Rhizosolenia morsa*, West., and *Tabellaria spp.*, fr.
Ennerdale	Desmids dt. (*Staurastrum jaculiferum*, *lunatum* var. *planctonicum*, West, *longispinum*, Bail.); *Sphærocystis Schrœteri* and *Peridinum Willei* ab.; *Rhizosolenia morsa* fr.
Buttermere	Desmids dt. (*St. jaculiferum*); *P. Willei*, *S. Schrœteri* and *Dinobryon cylindricum*, Imhof. ab.; *Tabellaria* spp. fr.
Crummock	Desmids (*Staurastrum annatinum*, C. and W., *Spondylosum pulchrum* var. *planum*, Wolle) and *Dinobryon cylindricum* dt.; *Botryococcus Braunii*, Kutz., and *Cœlosphærium Kutzingianum*, Näg. ab.; *Tabellaria* spp., *Melosira granulata*, Ralfs, and *Sphærocystis Schroetiri* fr.
Hawes Water	Diatoms dt. (*Tabellaria* spp.); Desmids ab. (*St. jaculiferum*); *Cœlosphærium Kutzingianum*, *Sphærocystis Schrœteri*, *Eudorina Elegans*, Ehr., and *Ceratium hirundinella*, Müll. fr.
Derwentwater	Diatoms (*Tabellaria* and *Asterionella* spp.) and *Dinobryon* dt.; *P. Willei* and mixed Desmids ab.; *Eudorina elegans* fr.
Bassenthwaite	Diatoms dt. (*Tabellaria* and *Asterionella*); Desmids and *Ceratium hirundinella* fr.
Coniston	Diatoms (*Tabellaria* and *Asterionella*) and *Ceratium hirundinella* dt.; *P. Willei* ab.; Desmids fr.
Windermere.........	Diatoms dt. (*Asterionella*); Desmids (*Staurastrum paradoxum* Meyen), *Tabellaria* and *Ceratium hirundinella*, ab.; *P. Willei*, *Melosira granulata*, *Sphærocystis*, *Eudorina* and *Oscillatoria Aghardii*, Gomont, fr.
Ullswater	Diatoms dt. (*Asterionella*); *Tabellaria*, *Dinobryon* and *Chroococcus* spp. ab.; *Sphærocystis*, Desmids and *Ceratium hirundinella* fr.
Esthwaite	Diatoms (*Asterionella*) and Myxophyceæ (*Oscillatoria*, *Anabœna* spp.) dt.; *Tabellaria* ab.; *Ceratium*, *P. Willei*, Desmids and *Eudorina* fr.

* Frequency symbols: *dt.* = dominant, *ab.* = abundant, *fr.* = frequent.

---

* "The Phytoplankton of the English Lake District," 'Naturalist' (London), 1909, p. 115.

† "Periodicity of Phytoplankton of some British Lakes," 'Journ. Linn. Soc.' (Bot.), vol. 40 (1912).

organisms, as recorded by the Wests or by the author. In view of the doubts expressed by some continental authors as to the reality of Desmid plankton—the percentage composition of the plankton is also given for August 23–30, 1920, when comparative samples were taken from all the lakes. These percentages are based on the number of individual organisms or colonies, *e.g.*, *Sphærocystis*, *Eudorina*, *Tabellaria*, etc.—the total number counted for each lake was over 1000. By comparison with other countings, these figures show rather low percentages of Desmids, and higher figures for Diatoms, except in the cases of Windermere, Ullswater, and Esthwaite. They are, however, the only figures available from collections taken at the same time.

Table VIII.—Percentage Composition of the Phytoplankton, August, 1920.

	Wastwater.	Ennerdale.	Buttermere.	Crummock.	Hawes Water.	Derwentwater.	Bassenthwaite.	Coniston.	Windermere.	Ullswater.	Esthwaite.
Desmids	*14*	*93*	*25*	*48*	19	7	1	4	11	5	7
Colonial Chlorophyceæ	*69**	2	*24**	*21*	10	4	0·5	9	8	1	5
Filamentous Chlorophyceæ†	7	2	18	2	1	4	6	4	6	5	1
Bacillariæ	9	1	9	1	*63*	*82*	*83*	*52*	*50*	*31*	5
Myxophyceæ	—	1	2	*23*	5	2	8·5	2	*19*	*30*	*64*
Dinobryon	—	—	13	3	—	1	—	—	2	27	14
Peridinieæ	1	1	9	1	2	—	1	26	4	1	4

* Almost entirely *Sphærocystis Schrœteri*, Chodat.
† Almost entirely Conjugatæ, especially sterile *Mougeotia*.

A comparison of these results fully justifies the conclusions that—

(1) The primitive lakes have a Desmid plankton in which *Peridinium Willei* and *Sphærocystis Schrœteri* are abundant, and Diatoms inconspicuous;

(2) The more evolved lakes have a Diatom plankton in which, on the whole, *Ceratium hirundinella* and *Eudorina elegans* are more typical;

(3) The three most advanced lakes have in addition a considerable element of Myxophyceæ, at times dominant in Esthwaite.

There is, therefore, a close similarity between the classification of the lakes on this basis, and that already made upon physical and chemical grounds. Since the characters of the plankton must depend very largely upon the salient features of the lake waters, such a marked similarity is to be expected, for it has already been shown that the properties of the lake waters are dependent upon the degree of physical evolution of the lake.

In the first place, the primitive lake waters are remarkable for their high $\frac{Na_2O+K_2O}{CaO+MgO}$ ratio, and only the waters of this type possess a predominant Desmid plankton. If it be assumed that the Desmid plankton requires such a high ratio of alkalies to other bases, it then becomes possible to explain not only the distribution of this type of plankton in this lake area, but also its presence in certain Scotch, Irish and Welsh lakes, for which data have been published. Moreover, the scarcity of Desmid plankton in European waters as a whole would then be due, on this assumption, to the scarcity of *pure* waters in which alkalies predominate (*i.e.*, excluding the sea and brackish waters). While it would lie outside the limits of the present paper to provide the data necessary to establish these statements, it may be assumed provisionally that Desmid plankton characterises waters with a high ratio of $\frac{Na_2O+K_2O}{CaO+MgO}$.

The abundance of Diatoms in the plankton of evolved lakes can also be correlated with the chemical characters of the lake waters. Since Diatoms have walls composed chiefly of silica,* they are obviously dependent on the presence of a certain amount of silica dissolved in the water. Thus a scarcity of silica—as in the primitive lakes—is accompanied by a scarcity of Diatoms, and these organisms are most abundant in those lakes containing the largest amounts of dissolved silica, *e.g.*, Windermere, Ullswater and Esthwaite. On the other hand a low $\frac{Na_2O+K_2O}{CaO+MgO}$ ratio is equally characteristic of fresh waters with a Diatom plankton and such waters are normally rich in nitrates. These factors may, therefore, be as necessary as the high proportions of silica.

A third element of marked interest in the plankton is the presence at times of abundant Myxophyceæ in Windermere, Ullswater and Esthwaite, well shown in the figures for August, 1920. It is noteworthy that these lakes have waters in which the organic content is normally *higher* than in the more primitive lakes, and it may be pointed out that Crummock Water has also a rather high organic content and a considerable element of Myxophyceæ. It is premature to say whether or no there is a *direct* connection between these facts, but it seems probable that they are in some way connected, as a dominance of Myxophyceæ is not unusual in waters having a high organic content.

A comparison of the bulk of the phytoplankton in these different types of lakes leads to the conclusion that *the greatest bulk occurs in the evolved lakes,* and that this is due primarily to the increased number of Diatoms (and Myxophyceæ). In this connection the results of Apstein,* taken with those of Brandt,† are of considerable interest. They show that in Holstein, lakes rich in nitrates contain the greatest bulk of plankton (chiefly Diatoms and Myxophyceæ), whilst scarcity of nitrates is accompanied by paucity of plankton. The water analyses show that this conclusion holds also for the English lakes, and it is therefore probable that Diatoms and Myxophyceæ are favoured by the presence of nitrates, provided their other habitat requirements are present.

---

* Whipple and Jackson record the fact that 49·48 per cent. of the dry weight of *Asterionella* is silica ('Journ. New England Waterworks Assoc.,' vol. 14, 1899).

Since it has already been shown that the $\frac{\text{alkali}}{\text{CaO}+\text{MgO}}$ ratio, silica, nitrate and organic contents of the lake waters are dependent upon the physical condition of the lake basin and drainage system, there are strong grounds for the conclusion that the development of the phytoplankton, both in quality and in bulk, in any of these lakes, is directly due to the degree of development of the lake basin. W. and G. S. West regard contamination of the drainage system by cultivation and sewage as an important cause of plankton and Diatom abundance. While this recognises the effect of the probable increase of nitrates caused by habitations and cultivations, it is not in itself a fundamental distinction. As weathering and erosion change the topography of the lake basin, there is a constant increase in nitrification and change in the characters of the surface waters. Farms and cultivation *follow* the development of soil and gentle slopes. They perhaps accelerate or increase the developmental reaction; they do not inaugurate it, and, therefore, *the stage of evolution of the lake basin must be regarded as being the fundamental factor affecting the distribution of the phytoplankton,* since it is upon this factor that the characters of the waters depend.

Finally, according to the views laid down previously, we may regard these lakes as illustrating a post-glacial development of the phytoplankton. The succcession would then become :—

Desmids dt. *Peridinium Willei* ab. *Sphærocystis Schrœteri* ab. *Rhizosolenia morsa* fr.	→	Diatoms dt. (*Tabellaria* spp.) Desmids ab.	→	Diatoms dt. (*Asterionella*) *Eudorina* ab. *Ceratium* ab.	→	Diatoms (*Asterionella*) and Myxophyceæ dt.

Fish—Economic Significance of Results.

The economic importance of all limnological studies is largely bound up with their bearing on the problems of fresh-water fisheries. The following account of the Lake District fisheries is based on that of Watson,[*] supplemented and modified by the opinions of local fishermen and a long personal acquaintance with the fishing on some of these lakes.

---

* 'Das Süsserwasserplankton,' Kiel und Leipzig, 1896.

† 'Wiss. Meeresunt.,' Kiel Komm., vol. 4, p. 215 (1899).

Fish are undoubtedly most abundant in the more evolved lakes and least so in the primitive ones; but this condition is due almost entirely to the numbers of coarse fish, perch (*Perca fluviatilis*), and pike (*Esox lucius*), which are especially abundant in Ullswater, Windermere, and Esthwaite, where they are increasing rapidly. The fish of the primitive lakes is undoubtedly the trout (*Salmo fario*), of which the largest numbers of well-grown fish probably occur in Crummock, Derwentwater, and Hawes Water. Pike and perch are absent from Wastwater, though the former were introduced some years ago without success. There are said to be a few perch in Ennerdale, but trout are the only abundant fish. On the other hand, trout are apparently decreasing rapidly in numbers in Ullswater and Windermere, and are practically extinct in Esthwaite. Char (*Salmo Willughbii*) occur in the deeper primitive lakes, and professional char-fishers say they also are decreasing in Windermere, as is known to be the case in Ullswater. Eels (*Anguilla vulgaris*) and minnows (*Leuciscus phoxinus*) are present in all the evolved lakes, and perhaps in Wastwater and Ennerdale also. It is certain, however, that there is a general progression in the lake series from the trout community to the perch-pike community, and the succession of these animal communities, therefore, closely parallels the development of the lake and its vegetation, as follows:—

Trout. Perch—Pike.
Primitive lakes. → Evolved lakes.

The economic value of fisheries may be assumed, roughly, to depend on two factors, the quantity of fish present, and their value from a commercial aspect, chiefly as food. From the former point of view, lakes like Windermere, Ullswater and Esthwaite rank first, since they undoubtedly contain the greatest numbers of fish per unit area. But, in food value, trout are the most important of the lake species, and, in this respect, the more primitive and intermediate lakes represent the more valuable fisheries, notably Derwentwater, Crummock and Hawes Water.

An increase in the abundance of fish is normally correlated with an increase in the abundance of plankton organisms, the phytoplankton forming the ultimate source of this increase. This correlation is so well established that we may regard the increase of fish in the more evolved lakes as being due to the physico-chemical conditions, which induce a more abundant phyto- and zoo-plankton in these lakes, and hence *the fundamental factor in the abundance of fish becomes in this case the stage of development shown by any particular lake.* Apart from the increase in the bulk of plankton, this factor operates in another way, for, as a lake develops, silts become richer and more abundant, and *rooted vegetation* more luxuriant. Hence there are increased areas on which epiphytic algæ can grow, and increased shelter and food for the smaller aquatic animals. The submerged vegetation of Esthwaite, as an extreme example, is literally teeming with life, and offers a marked contrast in this respect with vegetation from a primitive lake like Wastwater. Pond,* on different and theoretical grounds, also concludes that abundant rooted vegetation is favourable to fish production. He shows that rooted submerged vegetation draws its mineral nutriment chiefly from the substratum. Hence he argues that the seasonal decay of this vegetation enriches the water in salts at the expense of the soil, in this way favouring an increase in the bulk of the plankton. It must be remarked that Pond's assumption can only hold where organic decay is rapid and complete, and it is therefore more likely to operate in relatively evolved lakes where silts are abundant and rich than in waters where they are scarce, and the rate of organic decay is consequently slow. In the latter type of water, organic matter accumulates in an undecayed condition.

---

[*] 'The Lake District Fisheries,' London, 1898.

Kofoid,† however, concludes that the bulk of plankton (and hence of fish) is *inversely* proportional to that of the larger submerged plants. In the lakes to which he refers, the larger plants are almost entirely *Ceratophyllum*, a free floating form which must draw the whole of its mineral nutriment from the lake waters, and hence directly compete with the plankton. It is clear, from Kofoid's account of Flag Lake, that he recognises that an abundant *rooted* vegetation probably, on decaying, favours the production of a rich plankton. Hence his views are consistent with those advanced above, since the larger free-floating plants are absent from this lake area.

It would thus appear that the increase in rooted vegetation, in the bulk of the plankton, and in the abundance of fish, are all changes to be correlated one with another, and ultimately depend upon the topographic development of the lake.

No satisfactory evidence is as yet available to account for the decrease in numbers of trout in the evolved lakes. The indications are that trout food (mollusca, flies, larvæ and fresh-water shrimps) is most abundant in evolved lakes. It can only be suggested that the decline of this fish may be due to

---

* 'Rep. U.S. Comm. Fish.,' 1905, p. 485.

† 'Bull. Ill. State Lab. Nat. Hist.,' vol. 6, p. 95 (1899).

(i) the silting up of the stony feeding grounds or their covering with algæ (*e.g.*, *Cladophora*), as suggested by Weiss;[*] (ii) the development of summer "stagnation" and a deficiency of oxygen in the deeper waters of the evolved lakes. Both of these factors are apparently in operation, and both are dependent upon the other physical characters of the lake basins. Thus, though the intermediate links in the causal chain await further study, it is probably safe to assume that the changes in type and numbers of the fish in these lakes are intimately correlated with the physical development of the lake basins.

Summary.—The data presented show that a very close connection exists between the flora (and fishes) of the English Lakes and the physical and chemical conditions of their shores and waters. These lakes are of the same age (glacial), of similar origin, and lie among rocks possessing relatively uniform characters. It is therefore possible to attribute the differences they show to variations in the rates of erosion and sedimentation of the lake basins, due to inequalities in the durability of the underlying rocks. In distinguishing *rocky* from relatively *silted* lakes, a contrast is therefore made between *primitive* and more highly *evolved* lakes, and it becomes possible to describe the stages in the post-glacial development of a rock-basin. The conception has particular value biologically, since it permits the study of the post-glacial development of vegetation. The two extreme phases, here distinguished, differ in the following particulars:—

Extreme Lake Phases.

	Primitive.	Evolved.
Percentage of drainage system cultivable	5–8	17–45
„ lake shore rocky (to 9 m.)	73–47	27–12
„ *Isoëtes* and *Nitella*	85–74	52–30
„ *Juncus fluitans*	8–5	2–0
„ *Potamogeton* and *Naias*	½–2	30–55
Phytoplankton	Desmids dominant	Diatoms dominant
Fish	Chiefly trout	Chiefly perch and pike

Evidence is adduced for considering all these differences as ultimately dependent upon the physical condition of the lakes.

---

[*] Weiss, F. E., "Preliminary Account of the Submerged Vegetation of Lake Windermere, etc.," 'Proc. Lit. and Phil. Soc., Manchester,' vol. 53 (1909).

APPENDIX I.—Dimensions, Altitudes, and Geological Sites of the English Lakes.

	Length in miles.	Mean breadth in miles.	Area (square miles).	Greatest depth (feet).	Percentage area over 50 feet.	Altitude (feet).	Rocks underlying	
							Lake.	Drainage area.
Wastwater	3·00	0·37	1·12	258	77	204	Borrowdale Little granite	Borrowdale
Ennerdale	2·40	0·46	1·12	148	47·4	369	Granite Skiddaw	Borrowdale Granite
Buttermere	1·26	0·34	0·36	93	62·2	331	Skiddaw	Skiddaw
Crummock	2·50	0·40	0·97	132	73	321	Skiddaw	Skiddaw Little granite
Derwentwater	2·87	0·73	2·06	72	7	238	Skiddaw	Borrowdale
Bassenthwaite	3·83	0·55	2·06	75	6	225	Skiddaw	Skiddaw
Hawes Water	2·33	0·23	0·54	190	36	694	Borrowdale	Borrowdale
Coniston	5·41	0·33	1·89	184	62·9	146	Silurian	Borrowdale
Windermere	10·50	0·55	5·69	219	58	134	Silurian	Borrowdale
Ullswater	7·35	0·47	3·44	205	64·8	477	Borrowdale Skiddaw	Borrowdale
Esthwaite	1·50	0·33	0·51	70	—	217	Silurian	Silurian

APPENDIX II.—Water Analysis of English Lakes.

Figures—parts per million.

	Dissolved solids.			$Na_2O + K_2O$.	CaO.	MgO.	$\frac{\text{Alkalies}}{CaO + MgO}$.	Fe_2O_3. Al_2O_3	CO_2.	SO_3.	Cl_2.	SiO_2.	NO_3.	Hardness.*	
	Total.	Organic.	Mineral.											Temporary.	Permanent.
1. Wastwater	42·8	4·3	38·5	13·1	2·4	1·8	3·1	tr.	3·9	10·1	5·7	1·4	—	—	1·7
2. Ennerdale	30·6	5·6	25·0	7·3	2·4	1·2	2·0	tr.	2·4	4·6	5·7	1·4	—	—	1·4
3. Buttermere	52·5	6·4	46·1	15·4	2·8	2·3	3·0	0·4	3·2	13·9	6·6	1·4	—	—	1·8
4. Crummock	66·5	8·0	58·5	15·2	4·0	2·6	2·4	1·3	2·4	24·4	7·1	1·4	—	—	1·8
5. Hawes Water	47·1	4·3	42·8	12·3	4·0	3·6	1·6	0·1	7·1	5·7	7·1	2·8	tr.	0·3	2·0
6. Derwentwater	49·9	2·4	47·5	7·7	9·5	1·5	0·7	0·7	3·1	11·4	11·9	2·1	tr.	—	2·1
7. Bassenthwaite	57·0	6·1	50·9	8·3	7·9	3·5	0·7	0·4	5·7	14·9	7·1	2·8	0·4	—	2·0
8. Coniston	49·9	7·1	42·8	11·2	4·8	4·3	1·2	0·3	8·5	2·2	8·6	2·8	tr.	0·3	2·0
9. Windermere	59·8	10·8	49·0	5·4	10·1	1·4	0·5	0·4	6·4	13·1	8·5	3·3	2·0	1·0	1·8
10. Ullswater	54·2	11·4	42·8	10·6	5·6	3·1	1·2	0·1	7·8	4·2	7·1	4·3	2·0	0·3	1·7
11. Esthwaite	75·9	13·8	62·1	10·4	9·5	5·1	0·7	0·7	7·6	18·7	8·6	3·0	2·3	0·3	2·8
Mean 1–4	—	6·1	—	12·7	2·9	2·0	2·6	—	3·0	—	—	1·4	—	—	1·7
„ 5–7	—	4·3	—	9·4	7·2	2·9	1·0	—	5·3	—	—	2·6	tr.	0·1	2·0
„ 8–11	—	10·8	—	9·4	7·6	3·5	0·9	—	7·6	—	—	3·3	1·6	1·5	2·1

* As calcium carbonate—parts per 100,000.